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Provisioning adjustments by male and female fairy martins to short-term manipulations of brood size

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Summary

In biparental birds, the relative contribution of the sexes to feeding their brood (provisioning share) is sometimes reported to vary with brood size. However, the explanation for changes in provisioning share are often ambiguous (particularly in correlational studies), while the variation in findings between studies remains poorly understood. In this study we examined how short-term, within-pair manipulations of brood size (reduced, original and enlarged) affected provisioning rate in the fairy martin, *Hirundo ariel*. Following each manipulation, provisioning rates were monitored continuously for a two day period. Total provisioning rate increased when broods were enlarged and decreased when broods were reduced, though increases were inadequate to meet demand in enlarged broods because per chick feeding and growth rates declined. Both sexes responded similarly to brood size change over the course of the two days following the manipulation and there was no overall difference in provisioning share between treatments. Provisioning rate was correlated with wind strength (negatively) and ambient temperature (positively) but the response of the sexes to these variables was also similar. The absence of any change in provisioning share with brood demand suggests that alternative activities that could be traded-off against provisioning (e.g., self-maintenance) were similar for both sexes. Nevertheless, provisioning share may vary with the interval (i.e., hours, days, weeks) between the manipulation and measurement of provisioning, and these dynamics may contribute to explaining the inconsistent findings reported in the many previous studies examining the relationship between brood size and provisioning share.

Keywords: parental care, brood size, provisioning, feeding rate, fairy martin, *Hirundo ariel*.

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Introduction

In biparental bird species, the cost of brood provisioning is usually shared by the sexes, though the division of labour is often reported to vary considerably between pairs in the same population (Clutton-Brock, 1991; Ketterson & Nolan, 1994). Brood size typically has a strong influence on provisioning rates (e.g., Sanz, 1997; Lozano & Lemon, 1998; Nilsson, 2002; Hinde & Kilner, 2007) but the relationship may not always be similar for both sexes. For example, male share of provisioning has been reported to increase with brood size in a range of correlational studies (e.g., Carey, 1990; Lombardo, 1991; Filliater & Breitwisch, 1997; Carere & Alleva, 1998). However, such differences in relative contribution could be related to characteristics of the parents or environment rather than the size of the brood per se (Wright & Cuthill, 1990a; Stoehr et al., 2001). For example, high-quality males that invest heavily in provisioning may also hold territories with abundant food that allow females to produce larger clutches. Alternatively, older males may invest relatively more in care and also pair assortatively with females that produce larger broods (e.g., Petrie, 1983; Komdeur et al., 2005).

More compelling evidence for the influence of brood size on provisioning share comes from studies that show an increase in male share in response to experimental brood enlargement (Whittingham, 1989; Wright & Cuthill, 1990a; Moreno et al., 1995), though other studies report that the relative contribution of the sexes remains similar (Hegner & Wingfield, 1987; Smith et al., 1988; Wright & Cuthill, 1990b; Sanz, 1997; Verhulst & Tinbergen, 1997; Lozano & Lemon, 1998; Komdeur et al., 2002; Hinde & Kilner, 2007). Asymmetries in responsiveness may result if one sex has greater flexibility to adjust parental effort in relation to brood demand (Drent & Daan, 1980; Bart & Tornes, 1989; Markman et al., 1995). For example, males may have greater capacity to increase provisioning because they can reduce effort in other, male-specific activities such as nest defence (Hegner & Wingfield, 1987) or seeking additional social mates or extra-pair copulations (Westneat et al., 1990; Magrath & Komdeur, 2003). Moreover, provisioning share may be sensitive to the period of time since the manipulation was performed (i.e., minutes, hours, days or weeks). For example, both sexes may response initially to an increase in brood size, but one sex may be more able to sustain the elevated workload. Alternatively, one sex may respond more slowly to change in brood demand, which could occur if the sexes use different cues to

determine provisioning effort (Müller et al., 2007). For example, there is evidence from a number of species that the provisioning behaviour of females is responsive to a greater range of cues than for males (Kilner, 2002), potentially introducing a latency period between response of the sexes. Consequently, changes observed in parental effort following brood size manipulations may be dependent on the time between manipulation and measurement of effort, which may contribute to explaining the inconsistent findings in previous manipulative studies. It has also been suggested that such timescale differences may contribute to explaining the variation in parental responses reported across studies that have experimentally modified the level of care provided by one parent (Hinde, 2006).

In this study we explored the short-term consequences of brood size manipulation for provisioning rates in the fairy martin, *Hirundo ariel*. Fairy martins are socially monogamous, colonial nesting members of the Hirundinidae (Turner & Rose, 1989), and both members of the pair contribute extensively to incubation and brood provisioning (Magrath et al., 2002). Brood size manipulations (reduced, original and enlarged) were performed within-pair permitting us to assess changes in the contribution of the sexes without the variation between-pairs. To gain reliable estimates of change in provisioning, we recorded feeding visits continuously for two days following each manipulation using an electronic monitoring system. This allowed us to determine if the magnitude and/or timing of responses to brood size change differed between the sexes over the short-term. Further, we compared within-brood mass change of chicks across our brood size treatments to assess whether parents were limited in their capacity to meet brood demands.

Methods

Study population

The study was conducted between September and December, 2001 on three colonies of fairy martins near Booroorban (34°56′S, 144°52′E) in south-western New South Wales, Australia. Colonies were situated under small concrete bridges over the Coleambally irrigation channel. The channel was lined by a narrow belt of black box woodland, *Eucalyptus largiflorens,* and surrounded primarily by open grassland used for grazing sheep. These colonies comprised between 26 and 43 nesting pairs at their peak of activity, and were spatially separated by at least 8 km.

Monitoring the content of nests

Fairy martins construct bottle-shaped mud nests that have an extended tube-shaped entrance. We inserted an artificial plug into the sidewall of each nest near the main chamber, allowing us to examine the contents of all nests in the colony every two days (see Magrath, 1999 for details). Nestlings were assumed to have hatched (day 1) on the day of inspection if the chicks had damp or matted down feathers and/or eggshell remaining in the nest; otherwise they were deemed to have hatched the previous day (between inspections).

Trapping and banding

Most adult birds were captured before dawn inside their nests, where both sexes typically reside overnight after the clutch has been laid (see Magrath, 1999 for details). Captured birds were fitted with a numbered aluminium leg band to which a passive glass-encased transponder was glued (Trovan; 2×11 mm; 0.1 g). Adult females were distinguished from males by the presence of a brood patch, which is retained throughout the breeding season.

Remote monitoring of provisioning rate

Nest visits were documented using an electronic monitoring system. Individuals were identified from their transponders as they arrived at, and departed from, their nests. Each transponder emits a unique identification code when in the close proximity of a powered antenna. To detect a bird arriving or departing, the natural tube-shaped nest entrance was replaced with an artificial nest entrance of similar dimensions and external appearance, into which an antenna coil was incorporated. The artificial tube entrance was installed at least two days before monitoring of feeding rates commenced. Each arrival registered for an individual was considered to be a feeding visit. Possible, long-term effects of the artificial entrance on feeding rate were not examined but should not affect our findings because all experimental nests were treated in the same way. The accuracy of the system was evaluated by concurrent videotaping of six monitored nests, each for a 3-h period. Ninety-two percent of 163 arrivals were assigned correctly and the probability of an error was independent of parent sex.

Brood size manipulations

The brood size of 17 nests from three colonies ($N = 4$, 3 and 10) was manipulated experimentally. These broods hatched between October 29 and November 27 and had a modal size of three chicks (range 2-4) 10 days after hatching. Manipulations were conducted when broods were between 10 and 17 days of age, as a previous study revealed that brooding was minimal after day eight, and that brood feeding rates were generally quite constant over this period (Magrath, 1999). Each of these 17 broods was subjected to a 'reduced' (minus one or two chicks), 'original' and 'enlarged' (plus one or two chicks) size treatment in a random order. Chicks that were removed to create the reduced treatment were temporarily relocated to another nest, usually to create the enlarged treatment in another experimental brood of similar age (± 1 day). At each nest, brood size was manipulated every 48 h (generally between 1300 and 1400 h) and there was no overall pattern in the order of size treatment across broods (Kruskal-Wallis test, $p = 0.89$). Following each manipulation, nests were monitored for the following two days using the transponder system to record all parental visits, though complete data sets (all three treatments) were not collected for several nests because of brood reduction or failure of the monitoring system. We also recorded the body mass of each chick before and after each size treatment (to the nearest 0.1 g) to derive mass change (expressed in g/24 h).

Statistical analyses

At each nest, the rate for each parent (visits/h), total rate and rate per chick was calculated for each of five time periods of the day (0700-0900 h; 0900-1200 h; 1200-1500 h; 1500-1800 h; 1800-2000 h). These values were used as repeated measures of feeding rate for each pair of birds. For analysis we used the first ten complete time periods following each manipulation, which included the 1500-1800 h and 1800-2000 h periods on the day of the manipulation, all five periods on the following day, and the two morning periods on the third day. On each day of monitoring, we also recorded the maximum daily temperature and an estimate of wind strength at noon (1 = still, 2 = light, 3 = moderate, 4 = strong) to include in our models as environmental variables that were likely to influence feeding rate, and possibly the relative contribution of the sexes. Previous brood size treatment was also

included as a categorical explanatory variable in provisioning models to test for possible carry-over effects between the size treatments.

Data were analysed using multilevel mixed-modeling, following the procedure in MLwiN 2.0 (Rasbash et al., 2004), to account for their hierarchical and unbalanced structure. For these analyses, colony identity was specified as a random factor at level four, nest at level three, individual parent at level two and each repeat measure for that individual at level one. Normal response models were constructed, as the data for visit rate were distributed normally. Each model was derived using backward elimination of possible explanatory variables and their interaction terms. Brood size treatment was defined as a categorical variable with the control treatment as the reference category, allowing for specific comparisons between enlarged versus control and reduced versus control treatments, along with an assessment of the combined effect. The significance of explanatory variables was determined by calculating the change in model deviance (which approximates a χ^2 distribution) as each term was eliminated from the final model. Final models included a constant, together with any statistically significant ($p < 0.05$) explanatory variables. Non-significant interaction terms are not included in the model summary tables unless of specific interest.

Results

Total provisioning rate was lowest when broods were reduced in size and greatest when broods were enlarged (Table 1; Figure 1). However, the interaction between sex and brood size treatment was not significant, indicating that there was no overall difference in provisioning share between the brood size treatments (Table 1; Figure 1). Across all treatment groups, males visited broods at a higher rate than their partner (Table 1; Figure 1). Feeding rates were not related to previous brood size treatment for either sex (Table 1), suggesting the absence of substantial carry-over effects.

Provisioning rate tended to decline over the two-day period following manipulation (time since manipulation), though this pattern did not differ between brood size treatments and there was no significant difference between the response of the sexes over this period for any of the treatments (Table 1).

Provisioning rate was strongly correlated with wind strength (negatively), and to a lesser extent, maximum daily temperature (positively) and brood age

Table 1. Hierarchical model summary examining feeding rate of male and female fairy martins in response to within-nest manipulation of brood size (Treatment). Other explanatory variables included in the full model were previous brood size treatment, original brood size, time since manipulation (10 periods, see Methods), brood age, wind strength, maximum daily temperature and time of the day (5 periods, see Methods). Only significant terms $p < 0.05$) were retained in the final model. Specific comparisons between brood size treatments (e.g., Enlarged vs Control) are shown so differences between each treatment group can be assessed separately. Model effect size provided where $p < 0.10$. Model based on a total of 360 observation periods for 17 broods.

Explanatory variable	DF	χ^2	p	Model effect estimate (SE)
Brood size treatment	2	50.90	<0.001	
– Enlarged vs Control	1	6.66	0.01	+0.94 (0.36)
– Reduced vs Control	1	15.82	<0.001	−1.48 (0.37)
Sex (male vs female)	1	16.94	<0.001	+1.88 (0.46)
Wind strength	1	57.70	<0.001	−1.69 (0.22)
Temperature	1	6.57	0.01	+0.21 (0.08)
Brood age	1	4.63	0.03	−0.16 (0.08)
Brood size treatment * Sex	2	2.23	0.33	
– Enlarged vs Control	1	1.60	0.21	+0.88 (0.69)
– Reduced vs Control	1	0.01	0.92	+0.03 (0.71)
Previous brood size treatment	2	1.30	0.52	
Previous brood size treatment * Sex	2	0.28	0.87	
Time since manipulation	1	3.36	0.07	−0.13 (0.07)
Time since manipulation * Sex	1	0.20	0.65	
Time since manipulation * Treatment	2	4.03	0.13	
Time since manipulation * Treatment * Sex	2	5.41	0.07	
Hatching date	1	1.36	0.24	
Hatching date * Sex	1	0.06	0.81	
Time of day	4	5.11	0.28	
Time of day * Sex	4	2.06	0.72	
Original brood size	1	0.13	0.71	
Original brood size * Sex	1	2.94	0.09	+1.35 (0.76)
Wind strength * Sex	1	0.13	0.72	
Temperature * Sex	2	0.01	0.92	
Brood age * Sex	1	0.07	0.79	

(negatively) (Table 1). However, the effect of these variables did not differ between the sexes (Table 1).

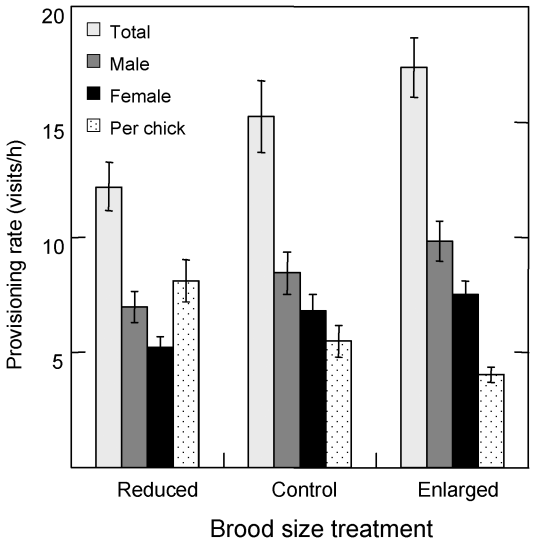

Figure 1. Total, male, female and per chick provisioning rates by fairy martins in relation to within-pair manipulation of brood size. Means and standard errors derived from raw data. Number of broods reduced = 14, original = 14, enlarged = 15.

Nestling mass gain was significantly related to brood size treatment, with chicks gaining most mass in reduced broods and least in enlarged broods (Table 2; Figure 2). This is consistent with the observed per chick feeding rate, which was highest in reduced broods (similar final model to that in Table 1 but with feeds/chick/h as the response variable; $+2.92$ feeds/h $\pm$ 0.27 (SE) vs original, $\chi^2 = 30.0$, $p < 0.001$; Figure 1) and lowest in enlarged broods (-1.43 ± 0.26 vs original, $p < 0.001$; Figure 1). Nestling mass gain was also negatively correlated with brood age and wind strength (Table 2).

Discussion

Brood provisioning rates were influenced by our short-term manipulations of brood size, declining markedly when the brood was reduced from its original size and, to a lesser extent, increasing when the brood was enlarged. However, these adjustments to provisioning rate were similar for both sexes as there was no within-pair difference in the share of provisioning between the three treatments. This result is similar to the majority of previous studies that have manipulated brood size experimentally (see Introduction), including the

Table 2. Model summary examining nestling mass change in relation to within-nest changes in brood size treatment. Other explanatory variables included in the full model were brood age, average wind strength, average maximum daily temperature and time of day. Only significant terms ($p < 0.05$) were retained in the final model. The model included 106 measurements of mass change for 53 nestlings in 17 nests.

Explanatory variable	DF	χ^2	p	Model effect estimate (SE)
Brood size treatment	2	36.3	<0.001	
Mean brood age	1	17.9	<0.001	−0.24 (0.05)
Average wind strength	1	65.4	<0.001	−2.24 (0.25)
Average temperature	1	0.62	0.32	0.04 (0.06)

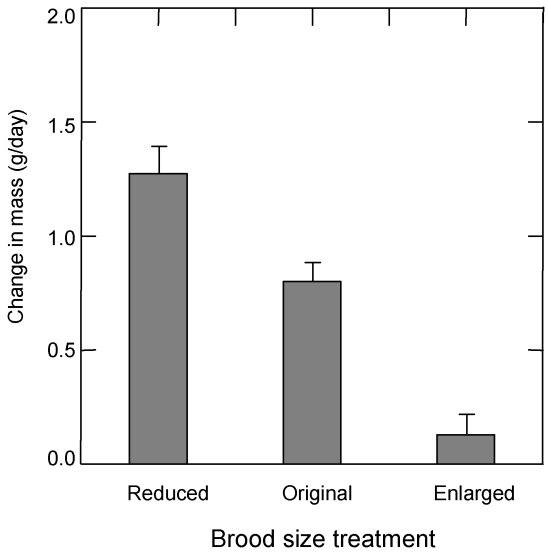

Figure 2. Mean daily mass change of fairy martin nestlings in relation to brood size treatment. Means and standard errors derived from model predictions after correcting for variation associated with brood age and wind strength. Number of broods reduced = 13, original = 13, enlarged = 12.

only other studies to examine within-pair adjustments to relative provisioning share in the short-term (Wright & Cuthill, 1990b; Komdeur et al., 2002). Moreover, we found no clear evidence for finer-scale response differences

between the sexes over the course of the two days following the brood size manipulations.

The increase in feeding rate to enlarged broods was apparently insufficient to fully compensate for the increased food demand of the larger brood. Both per-chick feeding rate and, more importantly, gain in nestling mass, were lowest in enlarged broods and greatest in reduced broods. These short-term growth effects may well have translated to differences in fledging mass, and possibly survival prospects, had the manipulation been imposed for the duration of the nestling period (Tinbergen & Boerlijst, 1990; Magrath, 1991). This apparent inability of parents to compensate adequately for brood size enlargement has also been revealed in other studies (e.g., Wright & Cuthill, 1990b; Markman et al., 1995; Rytkönen et al., 1996; Wright et al., 1998), and suggests that both parents may have been approaching their energetic limits.

The responses of the sexes to environmental conditions likely to influence the cost of brood provisioning were also similar. Wind strength had a dramatic affect on provisioning, with high winds reducing feeding rates by more than 50%. This effect is predictable for an aerial insectivore, as windy conditions will limit the abundance of flying insects (Williams, 1961), and presumably increase the difficulty of capturing those prey that are available. Moreover, nestling growth rate was retarded on days of strong winds, most probably because of the adverse affect of wind on feeding rate. If one sex were more capable (or willing) of responding to increases in brood demand, their relative contribution should have increased with wind strength. However, this was not the case as there was no interaction between sex and wind strength.

Feeding rate also increased with maximum daily temperature, suggesting that the cost of feeding was greatest on days of low temperature when insects are likely to be less active (Williams, 1961). Again, however, temperature did not affect relative provisioning share. Furthermore, any conflict between self-feeding and brood provisioning is expected to be most acute in the early morning and evening for small passerines (Avery & Krebs, 1984; Houston et al., 1988), as birds recover from, or prepare for, overnight fasting. However, our data show little evidence of variation in provisioning share over the course of the day. Overall, therefore, we found scant evidence that the sexes differed in their response to environmental fluctuations that may be expected to influence the cost of brood provisioning.

Similar responses by the sexes to changes in brood size and environmental conditions suggests that the sexes were equally capable (or willing) of adjusting to changes in brood demand. However, this does not necessarily mean that both sexes were responding to the same indicators of broods demand. A range of previous studies have identified sex differences in response to begging behaviour (Müller et al., 2007), while there is both empirical (Hinde, 2006) and theoretical (Johnstone & Hinde, 2006) evidence suggesting that parents may even adjust provisioning in response to their partner, independently of brood demand. In this study, the lack of an interaction between treatment and 'time since manipulation' suggests that adjustments to change in brood size occurred within hours of the manipulation and were then quite stable over the following two days. Consequently, it would be intriguing to examine the response of the sexes immediately before and after brood size manipulation. We detected no difference between treatments in provisioning share in the hour following manipulation, though our experiment was not designed to examine immediate responses, and these are likely to have been affected by our presence in the colony.

Likewise, it would be interesting to document provisioning share following brood size manipulation over the longer term. Possibly, females can sustain elevated provisioning levels for a shorter period, especially if they have invested more heavily than males earlier in the breeding attempt (e.g., incubation and brooding). In this study, the greater overall share of provisioning by males (across all treatments) may indicate that females were more constrained energetically at this stage of the breeding attempt because of greater previous investment (only females possess a brood patch and they perform 55% of incubation during daylight hours and the majority of chick brooding (Magrath & Elgar, 1997; Magrath, 1999)).

Provisioning rate is not the only variable that influences the amount of food delivered to the brood. Load size, type and size of prey can also have important effects on overall provisioning level, and several studies have revealed changes in diet composition with brood size (e.g., Tinbergen, 1981; Wright et al., 1998). In this study, the relative amount of food delivered by the sexes could have varied with brood size treatment, even in the absence of a shift in relative feeding rate, if changes in brood size influenced prey load, size or quality more in one sex than the other. We have no data to examine this possibility, but we are unaware of any studies that demonstrate

sex-specific effects of brood size on prey characteristics or load size. Moreover, most studies that have assessed both feeding rate and the total amount of prey delivered have found good concordance (e.g., Stoehr et al., 2001).

In sum, we suggest it may be rewarding to examine both short and long-term effects of brood size manipulation to help understand the dynamics of parental investment and negotiation. Indeed, the use of state-dependent dynamic game models has recently been advocated as the next step forward to help unravel the complexities of intra-familial interactions (Houston et al., 2005; Johnstone & Hinde, 2006). Moreover, differences in the timing of manipulation during the breeding attempt and the interval between manipulation and measurement of provisioning may help explain the inconsistent findings reported across the many previous correlational and experimental studies on the relationship between provisioning share and brood size.

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